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## VARIATION IN POLEMONIUM REPTANS

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*Polemonium reptans* L. varies as to height and habit of branching, number and shape of leaflets, size of corolla, shape of sepals, and density, length, and nature of pubescence. Two taxa within the complex should be distinguished—var. *reptans* and var. *villosum*—which in this paper will be referred to as *reptans* and *villosum*. The former is more variable than the latter. The writer believes that the variability of *reptans* is due to introgression, that the introgressant is the more stable *villosum*; variation within *villosum* may be coming from introgression from *reptans*.

In 1940, *villosum* was described as a variety of *P. reptans* (Braun, 1940). In 1942, Wherry reduced this to forma *villosum*, claiming that plants of this character “may appear almost everywhere over the range” (Wherry, 1942). In 1950, Davidson, in his monograph on the genus *Polemonium*, reduced *villosum* to synonymy with *P. reptans*, because he grew plants from seed of “glabrous and pubescent forms” furnished by Wherry (presumably from Pennsylvania), and found that “the plants grown from the two lots of seed were all quite glabrous, and the advisability of according taxonomic recognition to such an evanescent character is considered doubtful, even in the category of ‘forma’ ” (Davidson, 1950).

Unfortunately, Davidson obtained no seed of the glandular-villous *villosum* from the geographic area whence it had been

<sup>1</sup> The writer expresses thanks to Dr. Edgar Anderson for his encouragement and helpful suggestions during the progress of this study, and to Dr. Richard P. Goldthwait for glacial boundaries on the map.

reported. Examination of all material in the Gray Herbarium previous to setting up this "variety" revealed no specimens comparable to it. Subsequent examination of specimens in the herbarium of the Missouri Botanical Garden, the Ohio State University, the University of Pennsylvania, and the herbarium of E. T. Wherry has further demonstrated that typical *villosum* is represented only by specimens from a limited geographic area—Adams, Highland, Pike, and Scioto counties, Ohio, and Lewis County, Kentucky. Ten of the 70 specimens in the Ohio State Herbarium are *villosum*, all from Adams and Scioto counties.

That *villosum* comes true from seed is amply demonstrated by the large pure populations occurring in its restricted range—populations of hundreds of plants. It comes true from seed in the writer's woodland. All colonies occur near the western border of the Unglaciated Allegheny Plateau (Fig. 1), an area which has had a long and complicated physiographic and climatic history, an area known for the occurrence of disjuncts, and of species at margin of their range (Braun, 1928, 1951; Thomas, 1951; Wolfe, 1951). Before discussing the possible history of *villosum* and *reptans*, the characters of the two taxa will be contrasted; consideration of intermediate or intergrading forms will follow. Mass collecting or population sampling methods have been used.

The "Manual" descriptions of *Polemonium reptans* (and Davidson's also) doubtless include the intermediate forms, which here are omitted from the discussion of *reptans*; they do not include *villosum*.

The most constant diagnostic character of *villosum* is the densely glandular-villous inflorescence, in contrast to the "minutely puberulent" (Gleason, 1952) inflorescence of *reptans* (Fig. 2). The glandular hairs are multicellular, 0.5 to 1.0 mm. or more in length, and taper from base to glandular summit (Fig. 2E). In life, these glandular hairs may be seen without the aid of a lens, because of the conspicuous glistening glandular secretion present.

Stems and leaves of *villosum* are glandular-villous, but less densely so than the pedicels, except near the nodes. Glandular stem-hairs are often 1–2 mm. in length (Fig. 2C). The stems are not lustrous as are those of *reptans*. Hairs of the leaf rachis

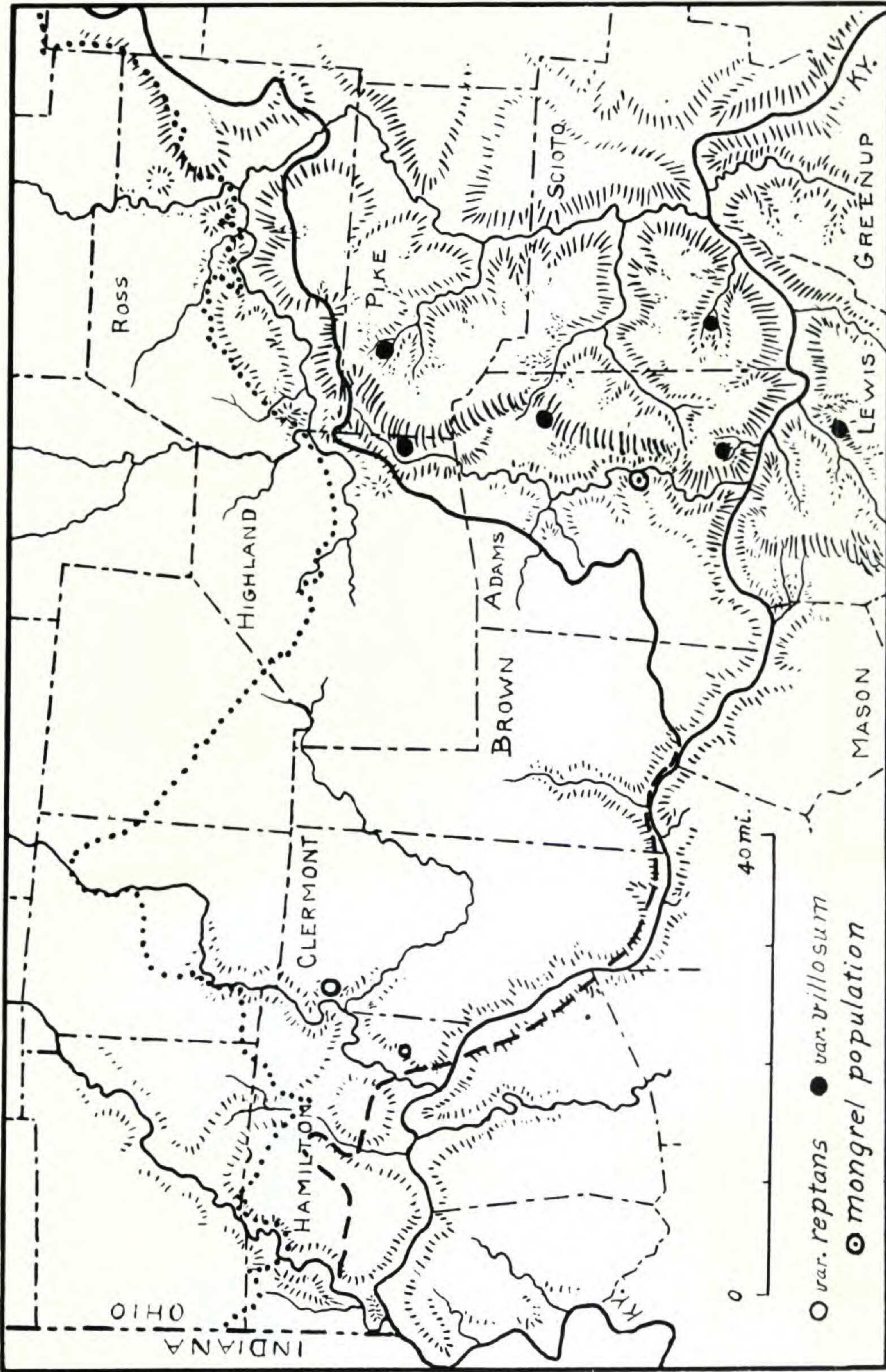


FIG. 1. Map of southwestern Ohio and adjacent Kentucky showing location of populations of *Polemonium reptans* L. studied; the larger circles indicate populations used in graphs. The higher and more rugged Allegheny Plateau is to the east, its western escarpment indicated by stronger hachures. The limit of Illinoian glaciation is shown by heavy full line (extending from upper right to Ohio River) and broken line (where less definitely known); limit of Wisconsin glaciation by dotted line. Glacial boundaries furnished by R. P. Goldthwait and (broken line) by J. Forsyth.

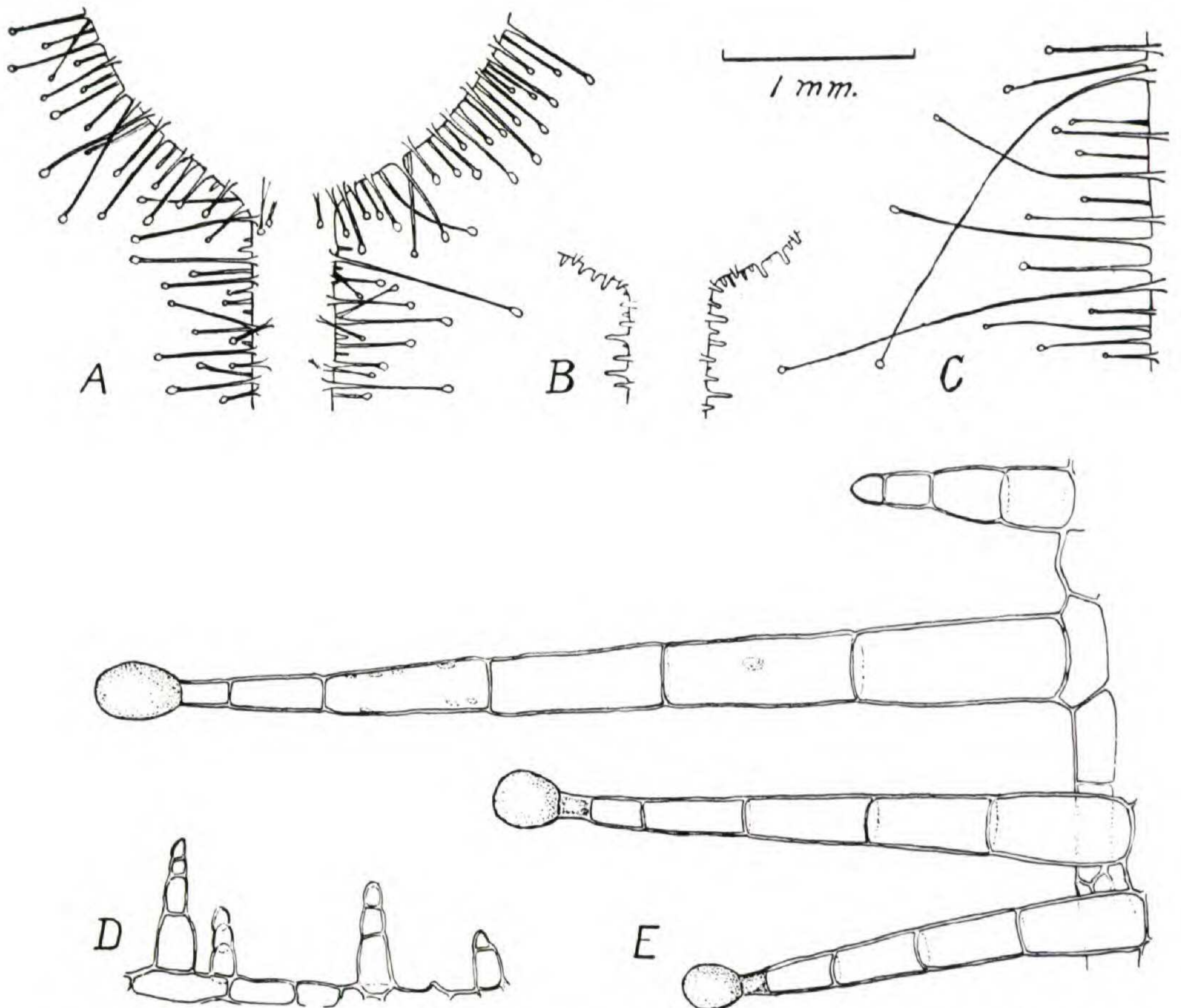


FIG. 2. Calyx, pedicel, and stem pubescence of *P. reptans* var. *reptans* and *P. reptans* var. *villosum*: A. Pedicel and lower part of calyx of *villosum*; B. Pedicel and lower part of calyx of *reptans*; C. Stem of *villosum*, just above lowest cauline leaf (A, B, and C in optical section; 1 mm. line shows scale); D. Greatly magnified pedicel hairs of *reptans* and E, of *villosum*. All drawn from living material.

are similar. Plants of *villosum* are so viscid that bits of humus and other foreign matter, and small insects are seen adhering to stems and pedicels. These help to give herbarium specimens of *villosum* their characteristic aspect. An odor of skunk, similar to that of certain western species of *Polemonium*, is noticeable if living plants have been enclosed, as when collecting in plastic bags, and, at times, when handled in the open.

In general, plants of *villosum* are lower than those of *reptans*, and the main stems diverge from one another at a wider angle.

Basal leaves of *villosum* tend to have fewer leaflets than those of *reptans*. The ratio of length to width of leaflets differs in the two. Leaflets of *reptans* are more than twice as long as wide; those of *villosum* mostly less than twice as long as wide (Figs. 3, 4). Differences in leaves in the inflorescence may be

less pronounced. Correlated with the broader and shorter leaflets of *villosum*, apical and basal angles are normally wider than those of *reptans* (Figs. 3, 4). Leaflets often are not "acute" as are those of *reptans*, the margins sometimes converging at angle of  $105^\circ$  or more, and often over  $90^\circ$  seldom less than  $75^\circ$ . Although the ranges of leaflet number and of length : width ratio overlap, populations of the two taxa are noticeably different in leaf aspect.

Flowers of *villosum* are smaller than those of *reptans*, 8–12 or rarely 13 mm. long, in contrast to 12–16 mm. long. The size differences of wide-open flowers (measured in the field) is more prominent: 11–17 mm. (av. 14 mm.) in diameter, as contrasted with 18–23 mm. (av. 19.5 mm.).

Many pedicels of *villosum* are shorter than the calyx, both in flower and fruit. The calyx lobes are shorter and broader, not "lanceolate to lance-triangular" (Fernald, 1950) as are those of *reptans*, but more deltoid, often almost an equilateral triangle in shape. The calyx of *villosum* is glandular-villous, especially toward base, and its margin glandular-ciliate (Fig. 2A).

In the field, *reptans* and *villosum* are so obviously different that they are readily distinguished. This has been emphasized more than once when the writer has been asked "what is the *Polemonium* in Adams County?" or told that one will not thrive under cultivation (as does *reptans*), or that "it is not worth growing, anyway." It is far less showy.

To demonstrate differences in pure populations of *reptans* and *villosum*, pictorialized scatter diagrams of the type devised by Anderson (1949, 1952, 1953) have been used (Fig. 4).

All parts of the plants of *villosum* are glandular-villous—pedicels and calyx, stems, and leaves. Such plants are represented on the pictorialized scatter diagram by solid dots, to contrast with the circles used for the essentially glabrous and non-glandular *reptans* (Fig. 4). Position of dots on this graph is based upon the ratio of length to width of median leaflets of cauline leaves, and upon pedicel-hair characters.

For the length : width ratio, the median pair of leaflets (or leaflets just below the middle, if number of pairs was even) of the lowest good cauline leaf were used. Cauline leaves near to the base of the stem and resembling basal leaves were rejected.

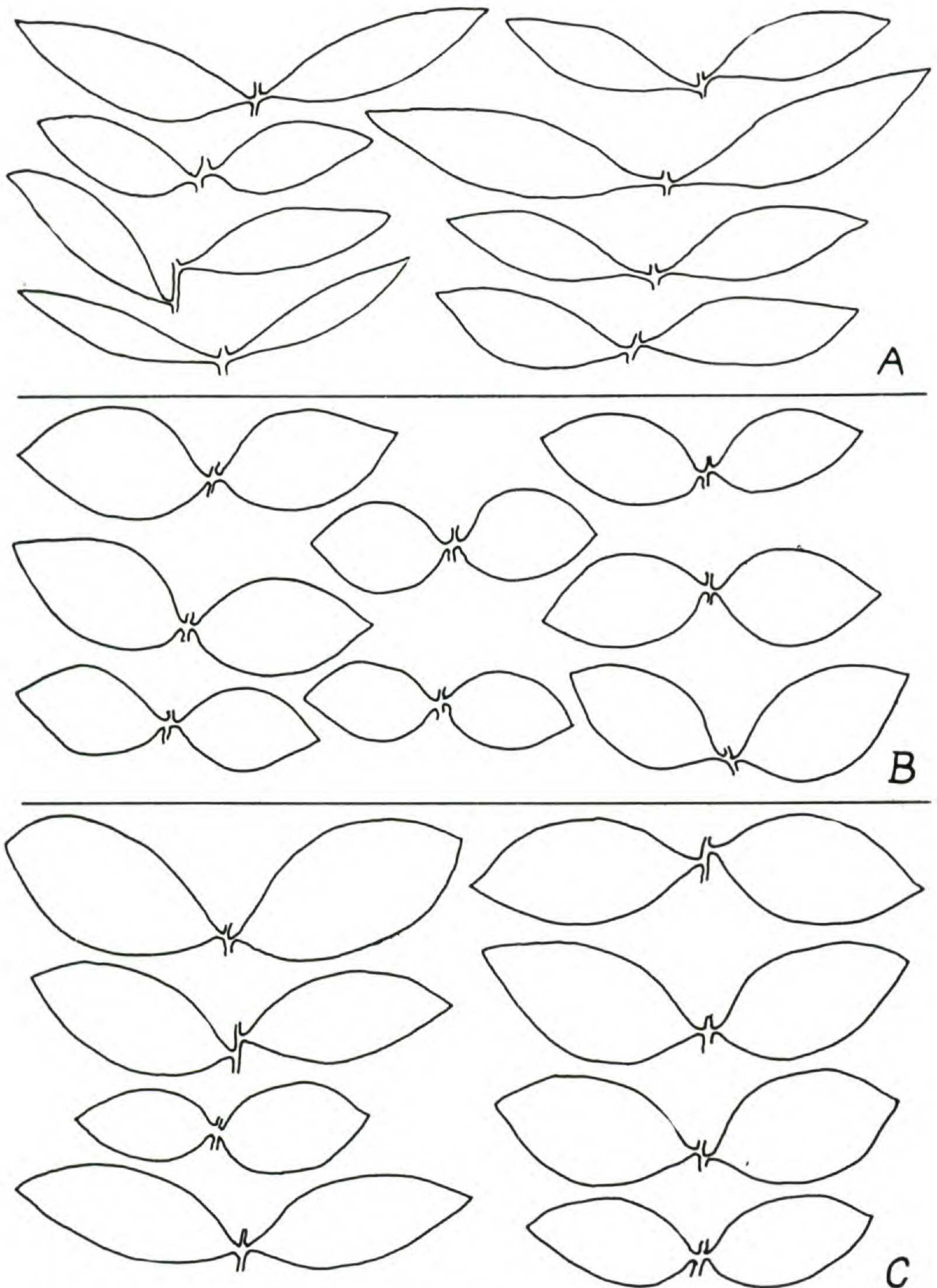


FIG. 3. Median leaflets (random sample) from basal leaves: A, of *reptans*, B, of *villosum*, and C, of a mongrel population.

The length and greatest width of both leaflets were measured, and the ratios obtained from the two leaflets averaged.

The pedicel score is based on length and character of hairs of the pedicel:

1. All hairs short and stubby, .05 mm. long; hairs short, but less blunt; or, occasional hairs to .2 mm. long scattered among short hairs.
2. Many hairs  $.25 \pm$  mm., to some .3 mm.
3. Many hairs  $.3 \pm$  mm. to some .4 mm.
4. Hairs .3, .5, and .7 mm., and also shorter hairs.
5. Many hairs .5 or .7 mm., some .8 or 1.0 mm., and also shorter hairs.

Hairs were measured by using an ocular scale ruled to half millimeters, using whole pedicels. Exact measurements on whole pedicels are not possible because hairs project at various angles. The use of smaller parts and higher magnification was impractical because of variation from place to place. Pedicels were scored in intermediate positions (as shown on the graph) in accordance with variations in length and dominance of particular lengths.

Characters used on the glyphs are ones which cannot be measured or scored as closely as can the length : width ratio or length and nature of pedicel hairs. Angles were measured by superimposing on the form to be measured paper sectors differing from one another by  $15^\circ$ , i.e., sectors  $30^\circ$ ,  $45^\circ$ ,  $60^\circ$ ,  $75^\circ$ ,  $90^\circ$ ,  $105^\circ$ . Apical and basal leaf-angles often do not express the immediate tip or base of the leaflet, but rather the angle at which the margins converge toward apex or base. As margins are often slightly convex, the exact angle could not be measured.

Stem pubescence varies from base to inflorescence, and from internode to node. The three-score system used is:

1. Stems essentially glabrous, or with scattered hairs.
2. Hairs widely spaced on internodes, more closely placed near nodes or toward base of stem.
3. Hairs dense, or very dense, and long, some 1 mm. or sometimes 2 mm. long.

A three-score system was also used for leaves:

1. Leaves glabrous except for a few hairs in rachis groove or on petiole margin toward base, and except for a very small area of short hairs in concavity of base of midnerve of leaflets.
2. Rachis thinly pubescent, more densely so toward base.
3. Rachis villous; both leaf surfaces pubescent.

The complete separation on the diagram (Fig. 4) of glyphs representing flowering individuals of the *reptans* population from

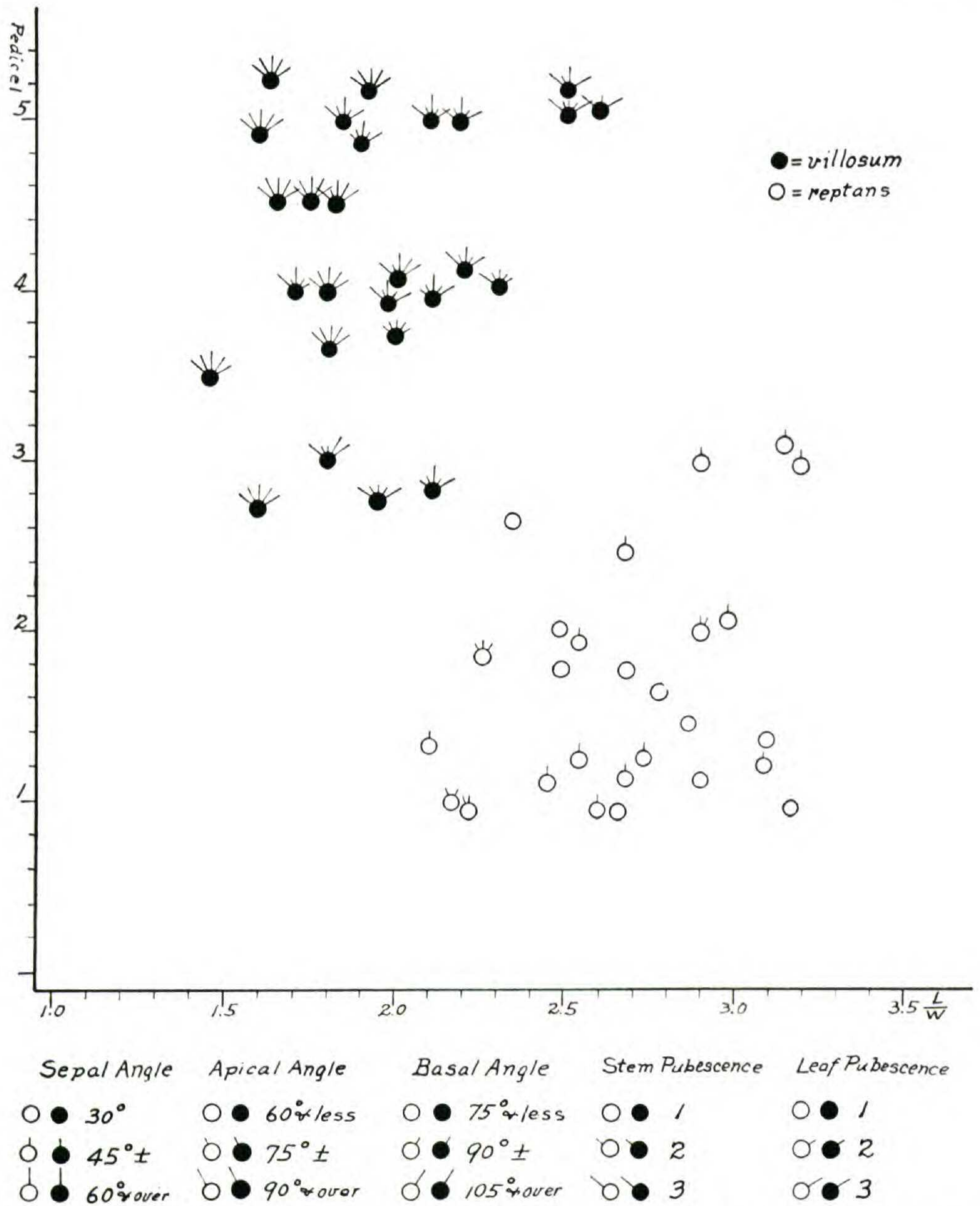


FIG. 4. Pictorialized scatter diagram of populations of *villosum* and *reptans*, based on characters of flowering plants collected in April. Horizontal axis: ratio of length to width of median leaflets of lowest good cauline leaf. Vertical axis: pedicel hairs, scored as described in text. Note complete separation of glyphs of the two populations.

those of the *villosum* population is evident. Almost as complete separation was seen on a diagram representing summer basal leaves, on which the glyphs were placed in relation to the length: width ratio and number of leaflets. Pubescence of leaf, and apical and basal angles were scored as in Fig. 4. Two entities were illustrated by these diagrams.

Some populations of *reptans* show slightly more variation than



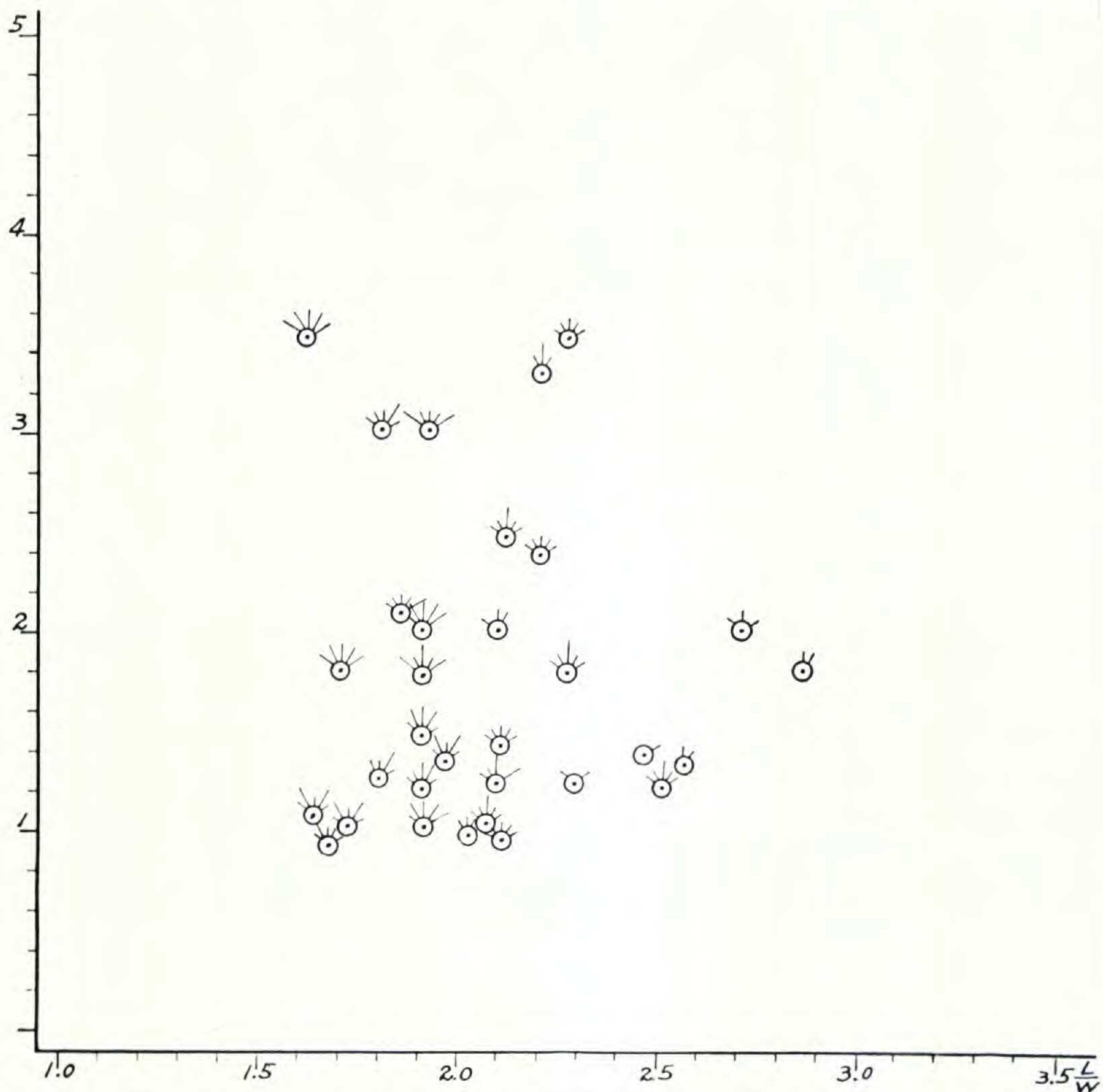


FIG. 5. Pictorialized scatter diagram of mongrel population, based on characters of flowering plants collected in April. Axes and glyph appendages as in Fig. 4.

the one illustrated by Fig. 4. Some herbarium specimens differ considerably from those of the population diagrammed, yet are obviously referable to *reptans*. What is the cause of this variation? Discovery of a mongrel population in which some plants resembled *reptans*, some resembled *villosum*, afforded an opportunity for analysis (Fig. 5). Open circles, with dot in center, are used in glyphs for this population, because such glands as may be present are inconspicuous and not evident under a 10 $\times$  hand lens as are those of *villosum*. Although a few of the longer hairs are structurally similar to those of *villosum*, the gland appears to be non-functional and the conspicuous tip is absent. All glandular hairs deteriorate in summer, and it is not possible to distinguish functional and non-functional glands at this season.

Comparison of Figs. 4 and 5 shows that the glyphs in Fig. 5 are not distributed like those of either *reptans* or *villosum*, that some are in the area of *reptans* glyphs, some in the area of *villosum* glyphs, and some in a position not occupied by either, but in the belt of low length : width ratio as well as in the position of puberulent rather than villous pedicels. Furthermore, there is a tendency for those of higher length : width ratio to be simpler—more like pure *reptans*—while those of lower length : width ratio tend to have more of the *villosum* characters. Such a tendency is indicative of hybridization. Although many plants resemble *villosum* in length : width ratio and in amount of pubescence, none has the characteristic glandular-villous inflorescence of that taxon. This character appears to be recessive, and to be controlled by different genes than is stem pubescence.

Comparison of summer basal leaves of *villosum* and *reptans* populations with those of the mongrel population brings out similar although less marked differences. Number of leaflets is not as distinctive a character as is pedicel-hair character. Nevertheless, the tendency toward *villosum*-like plants in the area of *villosum* glyphs, and toward *reptans*-like plants in the area of *reptans* glyphs was present in scatter diagrams of the mongrel population.

A high degree of sterility of some plants may be further evidence of hybridization. Failure of capsule development and accompanying excessive enlargement of calyx was noted in several specimens among the random samples.

The "connection between hybridization and disturbed habitats" has been summarized by Anderson (1949). This mongrel population of *Polemonium* occupies an area where man has "hybridized the habitat," an area on a wooded slope steepened many years ago when a road was built in the valley at its base. Typical *reptans* may have grown in this valley; and perhaps typical *villosum* occupied some of the ravines. The nearest known pure populations of the latter are in other valleys some four to six miles distant in an air-line and separated by high hills which interpose ecologic barriers. Typical *reptans* is much more distant (Fig. 1). Anderson has stated "it is only where man or catastrophic natural forces have 'hybridized the habitat' that any appreciable number of segregates survives."

Hairiness of stem and leaf, and low length : width ratio are prominent in the mongrel population. Glandular-villous pedicels are almost absent. This is precisely what is seen when hundreds of herbarium specimens of *P. reptans* (inclusive) are examined. Some are pubescent, some have broader leaflets than others, some have the short, "squatty" form of *villosum*, but none has the glandular-villous pedicels.

Hybridization, such as is clearly indicated by the mongrel population analyzed, may have taken place infrequently in the past. Some characters have been lost, some retained, in the ensuing back-crosses. The results of introgressive hybridization are evident over a wide geographic area, but pure or almost pure *reptans* populations prevail. And large pure populations of *villosum* exist in a limited geographic area. Why have these not been swamped by the widespread *reptans*? This would seem likely if *villosum* had always been surrounded by *reptans*.

The suggestion is here made that *villosum* is older than *reptans*, that the now restricted range of *villosum* is a remnant of a former more extensive and perhaps more northern range; that at some time during the Pleistocene this range was decimated, leaving only those populations south of the immediate effects of ice sheets. The distribution of existing populations of *villosum* correlates well with the disjunct occurrences of a number of species generally interpreted as relic distribution. Biotype depletion is a usual accompaniment of restriction of range. The uniformity of populations of *villosum* and their failure to spread suggest such biotype depletion.

The progenitors of *villosum*, as of other species of *Polemonium*, are still more ancient. In a chart "showing the postulated affinities between the recognized entities in *Polemonium*," Davidson (1950) indicates that *P. reptans* is related to *P. delicatum* Rydb. and more distantly, to *P. pulcherrimum* Hook., both of which are western species. *P. delicatum* of the Rocky Mountains of Colorado, Utah, Arizona, and New Mexico, is a glandular-pubescent species, which suggests closer relationship to *villosum* than to *reptans*. Another pair of species (or subspecies) displays a comparable east-west relationship—*P. Van Bruntiae* Britt. of circumscribed eastern range and *P. occidentale* Greene of the western mountains. Such relationships must be ancient. *P.*

*reptans*, in the restricted sense, is a widespread species found almost throughout the Deciduous Forest (mostly north of the Coastal Plain), and northward into Minnesota, central Wisconsin, northern Vermont and New Hampshire. It is common in the glaciated territory. The ancestral stock, from which *villosum* and perhaps *delicatum* were early differentiated, probably gave rise to other variants, and later, perhaps in late Pleistocene, to the glabrous *reptans*. Other lines of development in *Polemonium* include both glabrous and pubescent forms. Rapid spread of the glabrous *reptans* in late Pleistocene and post-Pleistocene time brought it into proximity with some of the relic populations of *villosum*, resulting in occasional hybridization, wherever the two came into actual contact. Thus *reptans* acquired some of its variability. Analysis of the scatter diagram (Fig. 4) supports this contention.

If the ten individuals most like each other and the ten least like each other on the basis of the measurements used on the horizontal and vertical axes of the graph be selected for determining average ray value for the other five characters (zero for no ray, one for a short ray, two for a long ray), it is found that perfect *villosum* would have a score of ten, and perfect *reptans* a score of zero. Actually, the ten individuals of *villosum* to the upper left in the diagram have an average ray value of 9.0; the ten individuals of *reptans* to the lower right have an average ray value of 0.4, both of which values are close to the perfect score. The ten *villosum* closest to *reptans* have an average ray value of 7.8; the ten *reptans* closest to *villosum*, a value of 0.9. This means that all seven characters, the two on the axes and the five on the rays, are tending to go together. Comparable analysis of the diagram of the mongrel population (Fig. 5) shows that the ten most like *villosum* have an average ray value of 7.1 (lower than the lower value of the *villosum* population); the ten most like *reptans* have an average ray value of 3.5. That is, the average values are intermediate, and the same tendency of all characters to go together which is seen in Fig. 4 is illustrated here.

Only further studies of *P. reptans* throughout its range will make possible the determination of centers of variability, of clines which could be the result of introgressive hybridization, of contamination of the glabrous *reptans* stock with the glandular-

villous stock of *villosum*. Such clines would give clues to time and direction of migration. The most prominent appears to extend in general westward of the area of the *villosum* populations in southern Ohio; another, less marked, is evident in southeastern Pennsylvania, where pubescence of many plants suggests that a relic population of *villosum* once existed thereabouts.

This situation in the *Polemonium reptans* complex is comparable to that of the wild black cherries discussed by McVaugh (1951, 52)—a common and widespread taxon (*Prunus serotina* subsp. *serotina*) ranging almost throughout the Deciduous Forest, in both glaciated and unglaciated areas, and a highly localized taxon (*P. serotina* subsp. *hirsuta*) occurring in areas where there are other disjuncts and rare local endemics. This latter is interpreted as more ancient than the glabrous and widespread *serotina*, and more closely related to western subspecies. The entire range of this complex, as of many other phylads, is somewhat V-shaped, with an eastern and western arm. *Polemonium* has a range comparable to that of the *Prunus serotina* complex, with representatives in Mexico, the East, and the West.

In view of the distinctness of *reptans* and *villosum* demonstrated by the pictorialized scatter diagram (Fig. 4), it is evident they should be maintained as distinct taxa. For the present, then, *Polemonium reptans* includes the two distinct entities, *P. reptans* L. var. *reptans* and *P. reptans* L. var. *villosum*, E. L. Braun. Whether the status of *villosum* should be changed to subspecies (which now appears suitable), or whether it should be maintained as a variety of *P. reptans* as originally described (1940) awaits further investigation. If the zoologist's definition of subspecies be accepted—"a geographically defined aggregate of local populations which differs taxonomically from other such subdivisions of the species"—then *villosum* is a subspecies, not a variety, which term is "limited to discontinuous variants within a single interbreeding population" (Mayr, Linsley, & Usinger, 1953). Certainly it is not a mere forma based on an "evanescent" character; it forms pure populations.—UNIVERSITY OF CINCINNATI.

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